

Generic Diversity in Phase of Rhythm in Myrmicine Ants

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Abstract: Few comparative studies in functional biology have been made at the genus level. In the tribe Myrmicini, the latest morning hour the workers are aboveground was compared for 58 species in 9 genera and the hour of mating flight for 40 species in 13 genera. In each case there is more difference in phase of rhythm among than within genera. When the possible influence of season, altitude, latitude, average rainfall, and average temperature is statistically removed by analysis of covariance, the generic diversity remains significant. This evidence suggests a taxonomic explanation of the diversity (as opposed to a strictly ecological or geographical explanation).

INTRODUCTION

Relatively few comparative studies in functional biology have been made at the genus level. In the ant tribe Formicini time of day both of mating flight and of worker foraging is much more alike from species to species within a genus than among genera (McCluskey, 1973). This correlation of behavior with taxonomic grouping suggested the value of studying more groups of ants. The present paper considers the tribe Myrmicini (broad sense) in another subfamily (Myrmicinae). It is again based on literature records.

DESCRIPTIVE COMPARISONS

Mating Flight

Figure 1 presents the midpoint flight hour for each species of each genus where records are available for at least two species. It can be seen first that the generic means range from 0700 to 1800 and second that the species flight hours tend to be similar within each genus. This generic diversity was tested by the circular distribution method of Watson and Williams (1956; cf. Batschelet

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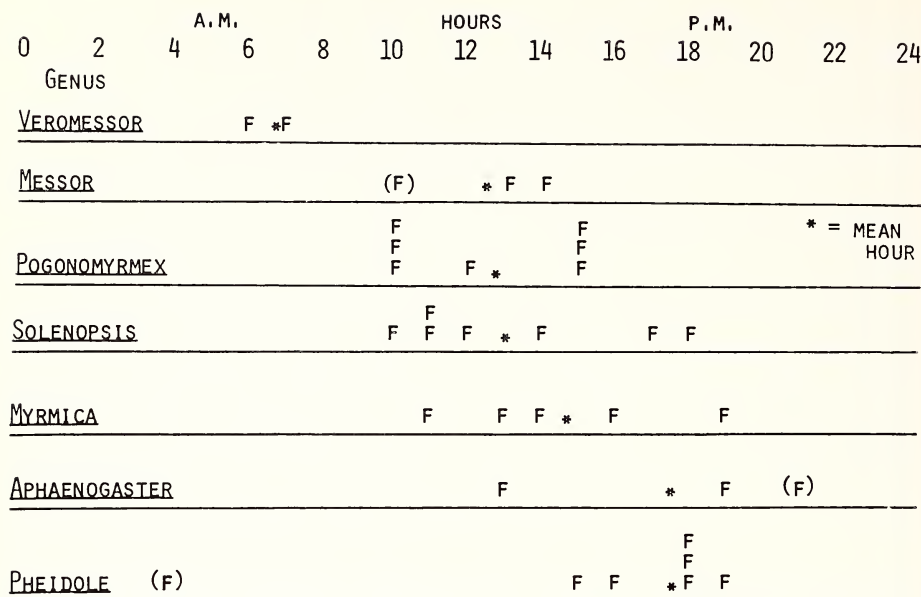


FIG. 1. Flight hours (all recognizable Daylight Time records were converted to Standard Time). Each F represents for one species the midpoint between earliest and latest literature records of flight; () indicate the most fragmentary records. Each asterisk shows the mean of the species midpoints for a particular genus. Following are the species and literature sources represented, including single-species records for 6 genera not plotted on the graph. Where personal communication (person. com.) is the source, the hour precedes name. *ATOPOMYRMEX*: *mocquerysi* (Wheeler 1922). *APHAENOGASTER*: *megommatus* (Smith 1963), *pythia* (Saunders 1969), *treatae* (Talbot 1966). *CAREBARA*: *junodi* (Wheeler 1922). *CAREBARELLA*: *bicolor* (Kempf 1969). *LEPTOTHORAX*: *mon-jauzei* (Cagniant 1968). *MESSOR*: *capitatus* and *structor* (Delage 1968, Meyer 1927), *semirufus concolor* (Mursaloglu 1957). *MYRMICA*: *laevinodis* (Donisthorpe 1927), *lobicornis fracticornis* (Kannowski 1959), *ruginodis* (Beare 1913; Brian & Brian 1955; Donisthorpe 1927), *sabuleti americana* (Kannowski & Kannowski 1957), *schenki emeryana* (Medler 1958; Talbot 1945, 1965). *PHEIDOLE*: *bicarinata* (1600, W. L. Brown pers. com.), *creightoni* (Gregg 1955), *megacephala* (Illingworth 1933, 1935; Williams 1935), *nari* and *sp. #10591* (Kusnezov 1962), *sitarches* (Wilson 1957), *pilifera pacifica* (1530, E. A. McCluskey pers. com.). *POGONOMYRMEX*: *badius* (Van Pelt 1953), *barbatus* (Wheeler 1910, 1917), *californicus* (Michener 1942), *imberbiculus* (Wheeler 1917), *maricopa* (Cole 1968), *occidentalis* (Nagel & Rettenmeyer 1973), *rugosus* (1515, F. Taylor pers. com.). *SOLENOPSIS*: *angulatus* and *sp. #10576* and *sp. #10577* (Kusnezov 1962), *invicta* (Markin et al. 1971), *molesta* (Mallis 1941; Talbot 1966; Wilson & Hunt 1966), *richteri* or *saevisima*? (Kusnezov 1962; Rhoades & Davis 1967), *xyloni* (1815, McCluskey unpublished; Wheeler & Wheeler 1973). *STENAMMA*: *brevicornis* (Kannowski 1958). *TETRAMORIUM*: *caespitum* (0700, G. C. & J. Wheeler pers. com.). *VEROMESSOR*: *andrei* (McCluskey 1963), *pergandei* (0730, McCluskey unpublished). An annotated table giving the details of support for Figs. 1 and 2 is available from the author.

1965, but only for a two-sample case): $F_{q-1, N-q} = [(N-q)(R_i - R)] / [(q-1)(N - R_i)] = 2.80$ and $P < .02$. ($N = 40$ species, $q = 13$ genera, R_i refers to the combination vector for all the species in each genus, and R refers to the combination vector of all genera.)

Worker Surface Activity

Whereas mating flights usually occur at a particular season for a given species, the workers come out of the nest over several seasons. In order to compare the various species most directly, I attempted to use only summer records from clear days. Since many of the literature records are incidental or otherwise fragmentary, the single item of information most useful for comparison was the approximate lateness of the hour the workers stay out of the nest in the morning.

In Fig. 2 a nocturnal species is indicated by an X representing out until "Dawn"; a species which stays out until the sun hits the nest is placed under "Sunshine"; etc. An intermediate time is indicated by an X between two adjacent columns. Every genus was included where records are available for at least three species.

The mean generic hour is seen to range from soon after the sun hits the nest (*Aphaenogaster*) to late morning (*Monomorium*); and there is a noticeable grouping of species. Arbitrarily scoring "Dawn" as 5 AM, "Sunshine" as 7 AM, "Midmorn" as 10 AM, and "Midday" as 1 PM, Watson and Williams' test indicates significant diversity ($P < .001$).

EXPLANATORY COMPARISONS

How might this generic diversity in phase of rhythm be explained? The data are too limited to answer an ultimate question such as whether the time relations are adaptive. But it is possible to ask preliminary questions. Is there a relationship at the genus level between phase and such gross measures of environment as altitude, latitude, average temperature, average rainfall, or season? (Current examples of studies at the species and microhabitat level indicating sensitivity to the environment include Bernstein, 1971; Levins et al., 1973; and Whitford, 1973).

For each observation locality cited I estimated the altitude (range, 0-2300 m), latitude (3° - 55°), average temperature (10° - 32°C) and total rainfall (2-75 cm) for the appropriate season (using mainly Hammond's Comparative World Atlas, 1963, and Nystrom's World Rainfall maps).

Analysis of covariance permitted consideration of the regression of the dependent variable on a number of independent variables (covariates) simultaneously. For the workers the latest-hour-out was used as the dependent variable, and altitude and latitude, or temperature and rain, as covariates. The generic diversity again appeared highly significant, even though possible altitude,

GENUS	DAWN	SUNSHINE	MIDMORN	MIDDAY
<u>APHAENOGASTER</u>	X X	(X) (X) (X) X *	(X) (X) X	
<u>VEROMESSOR</u>		(X)	X* X	(X) X X
<u>PHEIDOLE</u>	(X)	X	X* X	X
<u>MANICA</u>			X X *	X X
<u>NOVOMESSOR</u>			X X*	X
		* = MEAN HOUR	X X X X X X*	
<u>MESSOR</u>			X X*	X
<u>POGONOMYRMEX</u>		X	(X) X X *	(X) X X X X
<u>MYRMICA</u>			X X *	X X X
<u>MONOMORIUM</u>			X	X* X

FIG. 2. Worker surface activity. Each X represents one species and shows its nearest approach to midday. See text and also legend for Fig. 1. The following are represented: *APHAENOGASTER*: *ashmeadi* & *floridana* (Van Pelt 1958; Whitcomb et al. 1972), *fulva* (Park et al. 1931), *longiceps* (Brown 1955), *megommatus* (Cole 1966), *pallida* (Bernard 1968), *rudis picea* and *tennesseensis* (Park & Strohecker 1936), *splendida* (Tohmé 1969), *treatae* (Talbot 1953, 1966). *MANICA*: *bradleyi*, *hunteri*, and *mutica* (Wheeler & Wheeler 1970), *rubida* (Reichle 1943). *MESSOR*: *aegyptiacus* (Délye 1968; Sheata & Kaschef 1971), *alexandri* and *orientalis* (Tohmé 1969), *arenarius* (Délye 1968, 1971), *barbarus* (Buxton 1924; Forel 1928; Pickles 1944; Wheeler & Creighton 1934), *capitatus* (Delage 1968), *caviceps* (Délye 1964, 1968, 1969), *semirufus* (Bodenheimer & Klein 1930; Mursaloglu 1957). *MONOMORIUM*: *chobauti* (Délye 1968, *niloticoides* and *venustum* (Tohmé 1969), *salomonis* (Délye 1968; Kemp 1952). *MYRMICA*: *lobicornis* *fracticornis* (Dondale et al. 1972), *rubra* (Reichle 1943), *ruginodis* and *scabrinodis* (Brian 1955), *sabuleti americana*

TABLE 1. Analyses of Covariance. The contribution of rainfall and temperature might heavily overlap that of altitude and latitude as variables; therefore a second analysis, shown in (), was done, with rain and temperature replacing altitude and latitude as covariates

Source of Variation	DF	MS	F	P	
Workers (latest hour out) (58 species, 9 genera)					
Genera	8	12.7 (12.7)	5.5 (5.4)	<.001	(<.001)
Covariates	2	3.7 (3.7)	1.6 (1.6)	ns	(ns)
Altitude (or rain)	1	2.1 (5.4)	.9 (2.3)	ns	(ns)
Latitude (or temp.)	1	5.9 (1.4)	2.5 (.6)	ns	(ns)
Error	47	2.3 (2.3)			
Flights (deviation from midday) (40 species, 13 genera) (With season as months' deviation from August 1)					
Genera	12	8.7 (8.2)	2.5 (2.3)	<.05	(<.05)
Covariates	3	5.4 (4.1)	1.6 (1.1)	ns	(ns)
Altitude (or rain)	1	.7 (2.9)	.2 (.8)	ns	(ns)
Latitude (or temp.)	1	9.2 (2.9)	2.7 (.8)	ns	(ns)
Season	1	.0 (8.2)	.0 (2.3)	ns	(ns)
Error	24	3.4 (3.6)			
(With season as months' deviation from June 21)					
Genera	12	8.5 (7.4)	2.6 (2.1)	<.05	(<.10)
Covariates	3	7.0 (4.2)	2.2 (1.2)	ns	(ns)
Altitude (or rain)	1	.4 (2.2)	.1 (.6)	ns	(ns)
Latitude (or temp.)	1	11.8 (1.6)	3.7 (.5)	ns	(ns)
Season	1	4.6 (8.5)	1.4 (2.4)	ns	(ns)
Error	24	3.2 (3.6)			

latitude, average temperature and rainfall effects had been statistically removed by the analysis of covariance (see Table 1). The same was true if the possible complicating variables of the tropics were eliminated by performing the analysis for only the temperate zone species (which were the majority).

←

(Dondale et al. 1972; Talbot 1946, 1953), *schenki emeryana* (Talbot 1965). *NOVOMESSOR*: *albisetosus* (Wheeler & Creighton 1934), *cockerelli* (Wheeler & Creighton 1934; Whitford 1973), *manni* (Kannowski 1954). *PHEIDOLE*: *megacephala* (Carnegie 1960; Greenslade 1972; Levins et al. 1973; Steyn 1954), *morrisi* (Van Pelt 1958), *ridicula* (Creighton 1966), *saxicola* (Wheeler 1922), *sculpturata* and/or *crassinoda* and *sp. A* and *sp. Q* (Kemp 1952), *xerophila* (until 0630, R. Bernstein pers. com.). *POGONOMYRMEX*: *badius* (Carlson & Gentry 1973; Golley & Gentry 1964; Van Pelt 1953, 1966), *barbatus* (Box 1960; McCook 1879), *californicus* (Cole 1932; Michener 1942; Whitford 1973), *desertorum* (Whitford 1973), *magnacanthus* (Cole 1968), *maricopa* (La Rivers 1968), *occidentalis* (Headlee & Dean 1908; McCook 1882; Stevens 1965; Wheeler & Wheeler 1963), *owyheeii* (Cole 1934b; Willard & Crowell 1965), *rugosus* (until 0745, R. Bernstein pers. com.; Whitford 1973). *VEROMESSOR*: *andrei* (Creighton 1953; McCluskey 1963), *juliana* (Creighton 1953), *lariversi* (Cole 1963, 1966), *lobognathus* (Cole 1963; Wheeler & Wheeler 1959, 1963), *pergandei* (Cole, 1934a, 1963; Creighton 1953; Tevis 1958; Went et al. 1972; Wheeler & Creighton 1934), *smithi* (Cole 1963, 1966).

A similar search was made for an explanation of the diversity in flight timing. Flights, unless near midday, are generally either morning *or* afternoon, rather than bimodal like worker activity and like the environment. To relate both morning and afternoon flight times similarly to the middle of the "environmental" day, I used the difference between the hour of midday and the hour of either morning or afternoon flight as the dependent variable for regression studies. "Midday" was arbitrarily defined as 1300, since that is closer than noon to the hottest time of day according to the thermometer. Also 1345 divides the day into two equal halves with respect to the number of species flying. Further, 1307 is the average center of the midday hours avoided by workers; I calculated this from the 12 species (4 genera) where the records cited (legend of Fig. 2) are complete enough to show the worker bimodal activity pattern.

Season was included as an additional covariate, because flight records were used (Fig. 1) no matter what the season, rather than just summer records as for the workers. Season was measured two ways: as the difference between the date of the cited observation and either August 1 (to represent the average "heat center" of the summer) or June 21 (with the longest dawn- or dusk-to-midday interval). (Southern Hemisphere records were converted by 6 mo.)

Taking distance of flight hour from midday as the dependent variable, analysis of covariance shows the generic difference in timing to remain significant after removal of the effects of the covariates (Table 1). This is the more noteworthy because the morning-vs.-afternoon difference between genera is ignored in the choice of the dependent variable as simply the time from midday.

CONCLUSION

The records displayed here indicate generic diversity both of worker phase and of flight phase of rhythm beyond the effects of altitude, latitude, average temperature, average rainfall, and season. This is not to suggest that no relation with such variables would be found locally (e.g., temperate latitudes only), or in a microclimatic study, or at the species level. Nevertheless, at the genus level the evidence suggests a taxonomic explanation of the diversity (as opposed to a strictly ecological or geographical explanation).

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